



## **FINAL REPORT**

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### **Applications of Nonlinear Time Series Methods in Marine Ecology ONR, N00014-95-1-0034**

#### **LONG-TERM GOALS:**

The long-range aim of this project was to investigate the use of advanced nonlinear time-series methods in marine ecology. The ultimate aim is to provide predictive models for marine populations.

#### **TACTICAL OBJECTIVES:**

The near-term objectives of this project were as follows: 1) to compile a standardized collection of major marine ecological time series; 2) to refine advanced nonlinear time series methods for use with these data; 3) to identify the most promising of these marine data for analysis with these methods. The ultimate aim here was to demonstrate how such methods can be used on difficult problems to extract hidden information about the biological mechanisms and dynamical processes that are operating.

#### **APPROACH:**

Although ecologists have long held the belief that ecological systems are complex, consisting of many interconnected parts, they have not, for the most part, been studied as such. Ecological complexity has effectively been managed either by ignoring it or by defining it away through aggregation. Until recently, there has been no practical alternative to this problem; however, there is an emerging body of work on nonlinear time series analysis that may provide such an alternative. These methods allow one to extract from a single population time series, information about certain key characteristics of the larger ecosystem called "system invariants" that can be used to characterise the underlying dynamical process. More importantly, we have shown that these methods can be used to identify the underlying mechanisms and key variables that may be interacting to produce complex temporal behaviour (eg. see figure 1).

The immediate aim of this project was to compile a standardized collection of long-term ecological time series and to do a quantitative analysis of the most promising of these time series. It is reckoned that the house-keeping exercise in itself was of value in making the information more useful to other scientists.

## TECHNICAL ACCOMPLISHMENTS:

### 1) Data Acquisition:

We obtained spatially explicit time series data for an ocean system as well as spatially homogeneous data for a semi-closed reef system.

(a) Open Ocean Data: The time series information for the open ocean came from two main sources: daily temperature and salinity data from 12 fixed coastal monitoring stations along the California coast (1922-present; each station yielding two ~26,000-point time series, along with some shorter time series on fish impingement); and a large Calcofi data set containing biological/chemical/physical information that resolves to a spatial grid (1.2 GB). We have found that the Calcofi data set has been somewhat irregular in sampling frequency and location over that past 3 decades, but that it contains a stretch of regular monthly measurements from 1951-1969. Again, these time series measurements include a large variety of physical and biological factors. These data are reorganized and reformatted for easy cross reference and access.

(b) Reef Fish Time Series: In addition to the oceanic data sets, we have also obtained a set of fine-grained time series from Maria Milicich, an Australian investigator who works on fish recruitment in reef environments. These data include information on pomacentrid spawn, larvae and recruitment, as well as a variety of physical factors that may affect these phototropic fish (lunar phase, illumination, cloud cover, barometric pressure, wind speed and direction, temperature). The larval time series consists of 278 daily light trap censuses, along with concurrent physical measurements.

It was determined that this more manageable reef fish data set should serve as our test case for the applicability of advanced nonlinear methods to marine ecological time series. The reasons are as follows:

- (i) The data represent time samples taken at meaningful, regular intervals.
- (ii) The semi-closed nature of this particular reef system and the comprehensive spatial coverage in the samples taken, gave us more confidence that the time series data were indeed representative of the internal larval-reef dynamics.
- (iii) There was the potential here of shedding light on one of the most difficult problems in marine ecology: understanding the sources of episodic variability witnessed in larval recruitment dynamics.

### 2) Data Management:

We constructed a convenient and flexible data-browsing utility that accepts multivariate and spatial time series data in our standardized format. This utility has a convenient graphical interface and allows interspecies comparisons of spatial and temporal distributions. For example, one can animate the spatial abundance patterns of hake larvae across time to literally "see" the changes that took place across space and time. We have extended the multivariate capability of this utility so that easy comparisons and correlations with physical and chemical variables can be made.

### <sup>3</sup>~~X~~ Methods Development:

We developed two novel quantitative methods for identifying nonlinearity and hidden causation in time series data: residual-delay maps (with M. Casdagli, see fig 1), and multivariate forecast methods (Dixon et. al. SCIENCE).

### SCIENTIFIC RESULTS:

The main findings which we have uncovered in the larval reef-fish data are summarized in Dixon et. al (Science March 1999).

- i) A univariate analysis for larval pomacentrids indicates that complex and irregular daily fluctuations in abundance are actually a signature of a strongly nonlinear phenomenon. (Similar to figure 1, we have extracted the functional form of this nonlinearity with residual-delay maps).
- ii) Larval numbers are highly predictable on the daily time scale with nonlinear forecasting methods.
- iii) A nonlinear multivariate analysis, shows that wind stress on very young larvae (lagged 16 days) has a major influence determining larval abundance thirty days into the future. That is, with a nonlinear forecast model, wind stress lagged 16 days explains nearly 40% of the variance. A multivariate nonlinear model with 3 factors (wind, lunar phase, temperature) explains 64% of the variance in larval numbers whereas an equivalent multiple linear model explains only 5% of the variation.
- iii) The mechanism for the influence of lagged wind stress on larval numbers has a reasonable biological basis. The specific coupling between wind stress and larval numbers is shown to have a particular nonlinear functional form that was hypothesized in the larval ecology literature (eg. Davies et al 1991).
- iv) From a univariate perspective, daily spawning variation is well described by a linear autoregressive model (not nonlinear). This last finding combined with the first one is especially important because it may well explain why we often cannot find a good correlation (linear) between spawn and recruitment. These results show that this relationship is complicated by the intermediate step (the larval phase) which is essentially nonlinear. Thus, we may have some insight into the classic fisheries problem of why one cannot often find a good correlation between spawners and recruitment.
- v) The nonlinear forecasting model built for pomacentrids at Lizard Island has been shown to work well at predicting (as opposed to "postdicting"), larval abundances for this genus in Bimini, and for another distant reef. Such truly predictive models are an extreme rarity in ecology.

### SIGNIFICANCE:

The pomacentrid study suggests that the strongly nonlinear interaction of wind stress on larval fish survival may explain the resulting ambiguity in the spawner-recruitment relationship.

On a more general level, such nonlinearity in the larval phase, regardless of source, can help to explain the poor fit to classical models that is often seen in the spawner-recruitment relationship. This is one of the key problems in

fisheries science (see attached reprint).

In addition, we have demonstrated that our model has true out-of-sample predictability. Such demonstrations are extremely rare in ecology.

#### RELATION TO OTHER RESEARCH:

This project falls within my present research agenda which is the study of the structure and dynamics of complex natural systems. This work has been funded in part by endowment income from the John Dove Isaacs Chair in Natural Philosophy, Merrill Lynch Asia Pacific and Deutsche Bank. The generic methods developed for analysing time series (e.g. the RDMs) had applicability to my ONR-meterology project on atmospheric predictability (clear cross-fertilization between projects here).

#### PUBLICATIONS:

- (i) Hastings H. and G. Sugihara 1993 *Fractals: A Users Guide for the Natural Sciences*. Oxford University Press. 237 pages. (3rd printing)
- (ii) Translation of (i) above into German (Birkhauser).
- (iii) Yamazaki, H., G. Sugihara, G.J. Kirkpatrick and D. Kamykowski 1993. Is the photosynthetic process nonlinear? *Journal of Plankton Research*, 15:1297-1308.
- (iv) Sugihara, G. 1994 Nonlinear forecasting for the classification of natural time series. *Phil. Trans. Royal Society of London Series A.*, No. 1688, 348: 477-495. (invited address).
- (v) Sugihara, G. 1994 Prediction as a criterion for classifying natural time series. *World Scientific*. H. Tong ed.
- (vi) Sugihara, G. and A. Hobday 1995. One thousand words = one millipicture. *TREE*, 10(2): 89-90.
- (vii) Dixon, P., A. Hobday and G. Sugihara 1995. Review of fractals in science. *Jour. Math. Biol.*
- (viii) Sugihara G., W. Allan, D. Sobel, and K. Allan 1996. Nonlinear control of heart rate variability in human infants. *PNAS*.
- (ix) Hobday A. 1996. Body size variation in an intertidal limpet: the influence of tidal height, wave exposure and migratory behavior. *Jour. Exp. Mar. Biol. and Ecol.*
- (x) Hobday, A., K. Herbinson, and J. McGowan. 1996. Decadal scale stability in a Southern California fish assemblage. (submitted to *Ecology*).
- (xi) Bersier L. and G. Sugihara. 1997 Scaling regions for food web properties. *PNAS*. 94: 1247-1251.
- (xii) Sugihara, G. 1995. Blue chaos and locusts from the T'ang Dynasty, *Nature*.

- (xiii) Bersier L.F, and G. Sugihara and A. Hobday, 1995. A correspondence between two classical notions of community structure. *Rev. Suisse Zool* 102: 855.
- (xiv) Bersier L.F, and G. Sugihara 1996, Scale invariance versus scale dependence in food web properties. *Rev. Suisse Zool*. 103:779.
- (xv) Hastings H. and G. Sugihara 1996. *Fraktale Ein Leitfaden für Anwender* Spektrum Akademischer Verlag. 253 pages. (updated German translation of 1).
- (xvi) Sugihara, G., T. Allen, D. Sobel, and E. Allen 1996. Nonlinear control of heart rate variability in human infants. *PNAS (Medicine)* 93: 2608-2613.
- (xvii) Sugihara, G. L. Bersier and K. Schoenly 1997. The effects of taxonomic and trophic aggregation on food web properties. *Oecologia* 112: 272-284.
- (xviii) Bersier L. F. and G. Sugihara 1997. Scaling regions for food web properties. *PNAS* 94: 1247-1251.
- (xix) Bersier L.F., and G. Sugihara 1997. Species abundance patterns: the problem of testing stochastic models. *J. Anim Ecol.* 66: 769-774.
- (xx) Carney, H.J. and L.F. Bersier 1997. Nonlinear scale dependence and spatio-temporal variability in planktonic food webs. *Oikos* 79: 230-240.
- (xxi) Segundo, J.P., G.Sugihara, P. Dixon, M. Stiber, L. Bersier, 1998. The spike trains of inhibited pacemaker neurons seen through the magnifying glass of nonlinear analysis. *Neuroscience* (23 pgs).
- (xxii) Courchamp F, and G. Sugihara 1998. Biological control of alien predator populations to protect native island prey populations from extinction. *Ecological Applications*.
- (xxiii) Courchamp F, M. Langlais and G. Sugihara 1998. Rabbits killing birds: modelling the hyperpredation process.
- (xxiv) Courchamp F, M. Langlais and G. Sugihara 1998. Cats protecting birds: modelling the mesopredator release effect.
- (xxv) Courchamp F, M. Langlais and G. Sugihara 1998. Control strategies when both prey and predator are introduced.
- (xxvi) Bersier, L.F. P. Dixon and G. Sugihara 1999. Scale invariant or scale dependent behaviour of the link density property in food webs: a matter of sampling effort? *Am. Natur.* (in press).
- (xxvii) Sugihara G., M. Casdagli, E. Habjan, D. Hess, G. Holland, P. Dixon 1999. Nonlinearity in observed barometric pressure records: latitudinal gradients, dominant mechanisms, and improved forecasts. *PNAS* ( in press).
- (xxviii) Dixon, P., Milicich M., G. Sugihara, 1999. Episodic fluctuations in larval supply. *Science* 283: 1528-1530.